DEMOGRAPHY OF *CARDUUS PYCNOCEPHALUS* AND *C. TENUIFLORUS*

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ABSTRACT

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The biology of two annual thistles, *Carduus tenuiflorus* and *C. pycnocephalus*, was studied in the Manawatu and Hawkes Bay areas of New Zealand, respectively, over three years. Both species germinated mainly in the autumn and flowered only in the following spring. The exact time of germination varied between March and June, depending on weather. Survival to flowering ranged from 3-8% for *C. tenuiflorus* and 6-26% for *C. pycnocephalus*. Mean inflorescence output per plant varied from 2.6 to 10.0; seed number per inflorescence was dependent on inflorescence number per plant. Seed survival, to germination the following autumn, averaged about 12% in the Manawatu and was 38% in a single estimate in Hawkes Bay. While it was not possible to unequivocally separate the differences due to species, sites, and years, the two species were similar in their demography. Flowering in late autumn, reported at other sites, may represent a second generation of plants in a single year.

KEYWORDS: *Carduus tenuiflorus* - *C. pycnocephalus* - thistles - demography - annuals - flower initiation.

INTRODUCTION

Four European species of the genus *Carduus* have become naturalized in New Zealand, and all are weeds of pastoral land. The best known of the four is *C. nutans* (nodding thistle or musk thistle), a biennial which is widespread on the eastern sides of the North and South Islands. There has been much research worldwide into the biology of *C. nutans* (McCarty & Scifres 1969, Medd & Lovett 1978 a, b, Lee & Hamrick 1983, Popay *et al.* 1987). Less is known about the two annual thistles in the genus which occur in New Zealand: *C. tenuiflorus* (winged thistle) and *C. pycnocephalus* (slender winged thistle), even though both are widespread in New Zealand (Garnock-Jones 1987), and may at times displace significant amounts of pasture (Kelly & Popay 1985, Bourdot & Kelly 1986). The fourth species, *C. acanthoides*, is a biennial which is only common in the top half of the North Island.

In this paper I give the results of three years' study of *C. tenuiflorus* and *C. pycnocephalus* at two sites in the North Island of New Zealand. Firstly, the basic biology and demography of the species are described. Secondly, the two species are very similar taxonomically, so I wanted to find out whether there were any major demographic differences between them. Thirdly, both species typically flower in late spring, but there are occasional reports and herbarium records of flowering plants in early spring or late autumn. Those records are related to detailed data on flowering times in the field, and to previous work on the control of flower initiation in *C. tenuiflorus* (Staig 1986).

MATERIALS AND METHODS

The study was carried out at two sites in the lower North Island. One was on Midland Road (175° 43′ E, 40° 15′ S), 18 km north-east of Palmerston North in the Manawatu. The area receives an average rainfall of 900 mm, evenly

distributed through the year. The study site was in permanent pasture on a north-facing slope of about 15°, and was centred on a patch of *C. nutans*, which is uncommon in the Manawatu. *C. tenuiflorus* was common at the site, and there were occasional *Cirsium vulgare* (scotch thistle). Five permanent transects were established in July 1984. Each was 0.5 m wide and 10 m long. A recording frame was located over steel pegs sunk into the ground, and a T-square was used to record the locations of all thistle plants within the transects to an accuracy of ±1 mm.

Censuses were carried out about every six weeks. At every census the length of the longest leaf of every surviving thistle was recorded. As soon as any stem elongation was observed, in the first stages of transition from a rosette to an upright flowering plant, the thistle was recorded as having bolted. During flowering, the number of inflorescence buds, open inflorescences and inflorescences with ripe seeds were noted for each plant. This allowed the total number of inflorescences produced by each plant over the season to be determined. The number of inflorescences per plant was log-transformed to correct skew before calculating means for each population for purposes of hypothesis testing. Where the interest was in average or total seed outputs, the arithmetic mean of the number of inflorescences was used.

New seedlings were recorded in all five transects until June 1985. After that time new plants were recorded in only the first three of the transects until February 1987, when recording of new plants ceased. Once a seedling had been recorded in any of the transects, it was followed at successive censuses until it had died. Recording was completed in February 1988.

The second site was on Argyll Road (176° 34′ E, 39° 54′ S), 13 km north of Waipukurau in Hawkes Bay. The area receives an average rainfall of 950 mm per year, but is normally hot and dry over the summer and has an annual moisture deficit of 100-200 mm. The study site was in a permanent grass paddock of gentle slope (about 5°) which has been the location for a number of studies on thistle biology (Edmonds & Popay 1983, Popay *et al.* 1984, Kelly & Popay 1985, Popay & Kelly 1986). Both *C. nutans* and *C. pycnocephalus* were common in the area; *C. tenuiflorus* and *Cirsium vulgare* were present but uncommon. *C. tenuiflorus* made up less than 5% of the flowering annual *Carduus* at the site, and no *C. tenuiflorus* flowered in the transects during this study. It is possible that a few *C. tenuiflorus* seedlings germinated in the transects and were recorded as *C. pycnocephalus* (since the seedlings of the species cannot be distinguished), but this would have been rare and would not be expected to alter the results significantly.

At Argyll, five permanent transects identical to those at Midland were established in August 1984. Census frequencies and methods were similar to those at Midland. All new germination was recorded in the five transects until March 1985; from then until April 1986, new plants were mapped and followed in only two transects, and thereafter only established plants were followed until the last *C. pycnocephalus* died in December 1986.

To estimate the number of seeds (technically, achenes) per inflorescence, ripe inflorescences were collected from near to the permanent quadrats. At Midland 103 inflorescences were collected on 20 December 1984; at Argyll 107 inflorescences were collected between 28 November and 6 December 1984. In the laboratory, the inflorescences were cut in half and the receptacle diameter, the number of ripe seeds, and any attack by nodding thistle receptacle weevil (*Rhinocyllus conicus*) were recorded. *Rhinocyllus* was not present at Midland.

Seed weight was determined for 20 filled seeds of each species, taken from the inflorescences described above. The seeds were weighed individually to the nearest 0.1 mg.

To measure the survival of seeds from release to germination, at Midland 550 *C. tenuiflorus* seeds collected on 19 December 1985 were sown on 21 January 1986 into seven marked 0.1 m by 0.1 m squares in a random pattern, in lots of 25 (two replicates), 50 (two), 100 (two) and 200 (one replicate). The other 18 squares in the quadrat, which had no seed added, were used as controls to estimate background levels of germination. New seedlings were recorded in each square until February 1988. At both Midland and Argyll, seed survival was also estimated indirectly, by comparing the number

of seeds which ripened on plants in each 10 m by 0.5 m transect in spring, with the number of seedlings emerging there over the following year. This second method depended on the assumption that additions to and removals from the seed bank of each species would, on average, cancel out. Work on *C. nutans* at Argyll and in the Waikato has shown that seed in the upper soil layer disappears fairly quickly, and that over two years the seed bank did not vary much in size (Popay & Thompson 1980).

To plot survival of new seedlings through to flowering, each cohort (all the seedlings appearing over one inter-census interval) was treated separately. The large cohorts which appeared in autumn were plotted as single groups. The smaller cohorts which germinated at other times (in winter, spring and summer) were grouped together, since each cohort was too small for separate analysis.

RESULTS

GERMINATION

For both *C. tenuiflorus* and *C. pycnocephalus* the majority of seedlings germinated in the autumn (between February and May), generally over a period of less than two months (Fig. 1). The exact timing of this autumn flush of germination depended on the onset of wet, cooler weather after summer. The date when 50% of cumulative total germination was reached ranged from 8 March for *C. pycnocephalus* at Argyll in 1985, to 15 May in 1985 and 17 June in 1986 for *C. tenuiflorus* at Midland.

Few seedlings were observed to emerge in spring, and very few over summer (for example, new seedlings were never found at any census in December).

SURVIVAL AND THE TIMING OF FLOWER PRODUCTION

The survival of each major autumn-germinating cohort is plotted in Fig. 2. Mortality was very high for young *C. pycnocephalus* plants at Argyll, especially for the cohort germinating in March 1985. At Midland, mortality rates in *C. tenuiflorus* were generally lower. Rosettes began to bolt in October-November, and about 80% of flowers were produced over the last two weeks of November and the first two weeks of December (Fig. 1). Only occasional plants were still alive and flowering into January. No plants were seen to flower at the study sites between March and November of any year.

The overall percentages of seedlings in different cohorts which managed to set seed, or which bolted but failed to ripen any seed, are given in Table 1. Generally, a higher percentage of seedlings survived to flowering for *C. tenuiflorus* than for *C. pycnocephalus*. Plants which germinated in the main autumn flushes had significantly higher probabilities of setting seed than those which germinated at other times (for *C. tenuiflorus*, $X^2 = 40.67$, $df = 3$, $P < 0.001$; for *C. pycnocephalus*, $X^2 = 17.86$, $df = 2$, $P < 0.001$), although at Argyll there was no difference in survival between the autumn 1985 cohort and all the non-autumn seedlings ($X^2 = 0.238$, $df = 1$, *ns*).

INFLORESCENCES PER PLANT

There was significant variation from year to year at both sites in the mean number of inflorescences per plant (Table 2). There were no consistent differences between sites or species in mean number of inflorescences. The causes of the variation will be discussed further in a subsequent paper.

SEEDS PER INFLORESCENCE

The number of seeds per inflorescence ranged in 1984 from 20 down to zero. For both species combined, a regression equation using three independent variables (the number of inflorescences per plant, the inside diameter of the receptacle, and whether or not, for *C. pycnocephalus*, the inflorescence was attacked by *Rhinocyllus*) explained most of the variance in the number of seeds per inflorescence (71.9%). In this stepwise model, species (*C. tenuiflorus* or *C. pycnocephalus*) did not reach the level of significance required for inclusion; in other words, for a given number of inflorescences per plant and receptacle diameter, after allowing for weevil attack at Argyll, there was no difference between the species in seed output per inflorescence.

A second regression was calculated, also based on the data for both species, which pre-

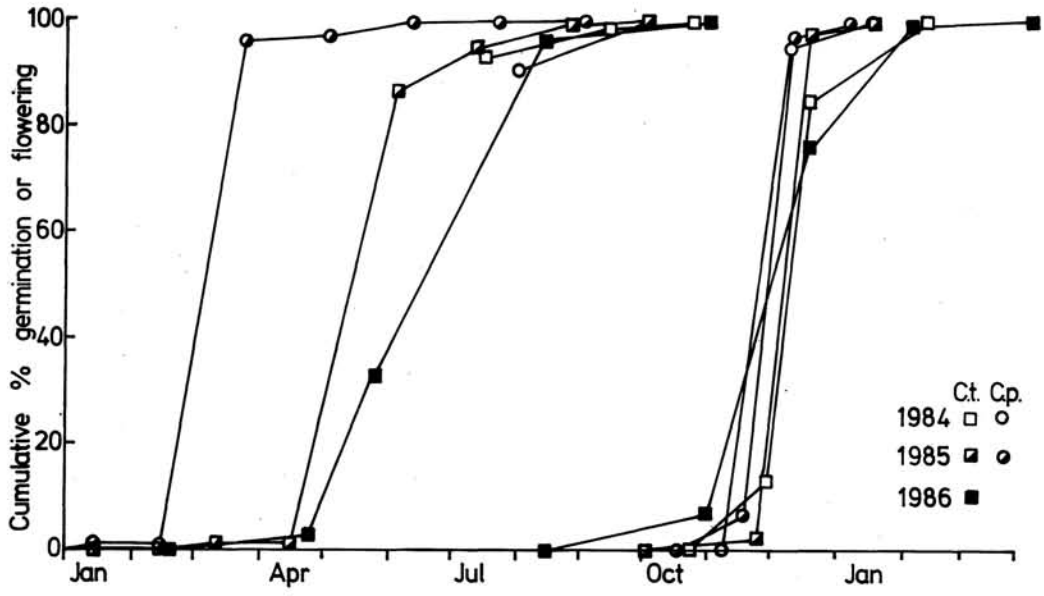

Figure 1. Cumulative germination (February - July) and flower ripening (October - January) for populations of *Carduus tenuiflorus* at Midland in 1984-86 and *C. pycnocephalus* at Argyll in 1984 and 1985.

dicted seed number from only the number of inflorescences per plant. Although the regression based on three independent variables explained more of the variance, inflorescence number was the most important of the three (and the easiest to measure, since it did not require destructive sampling). The calculated regression was: $y = 0.250 + 7.891(\log_{10} x)$

This equation explained almost half the variance ($r^2 = 0.4822$, $n = 210$, overall $F = 195.7$, $P < 0.001$).

To estimate the mean number of seeds per plant at each site in each year, the arithmetic mean of the number of inflorescences per plant was inserted into the equation above. Mean seed output for *C. tenuiflorus* in 1984, 1985 and 1986 was 249, 43.5 and 23.2 seeds per plant respectively. At Argyll for *C. pycnocephalus* in 1984 and 1985 the means were 71.7 and 276 seeds per plant.

SEED WEIGHT

Seeds of *C. pycnocephalus* were significantly heavier (mean = 6.0 mg $\pm$ *s.d.* = 1.34, $n = 20$) than seeds of *C. tenuiflorus* (mean = 3.7 $\pm$ 0.56, $n = 20$) according to a t-test ($t = 7.06$, $P < 0.001$).

SEED SURVIVAL

In the seven 0.1 m by 0.1 m squares at Midland where 550 *C. tenuiflorus* seeds were sown in early 1986, only seven seedlings had germinated by February 1988. In 18 adjacent squares where no extra seed was sown, two seedlings (0.11 per square) emerged. Assuming a similar level of background germination from unsown seed in the sown area, overall only 1.1% of the sown seeds germinated in the following two years.

The ratio between seeds set in each transect in one year and germination in the following year

Species	Cohort	% seeded	% bolted	N
C. tenuiflorus	Autumn 1984	26.4	14.1	284
	Autumn 1985	15.3	14.6	782
	Autumn 1986	15.2	23.7	565
	All others	6.1	14.3	231
C. pycnocephalus	Autumn 1984	7.9	5.8	429
	Autumn 1985	2.8	0.1	879
	All others	3.6	3.6	139

Table 1. Percentage of seedlings, in different cohorts of *Carduus tenuiflorus* at Midland (Manawatu) and *C. pycnocephalus* at Argyll (Hawkes Bay), which set seed or bolted without setting seed. For significance testing of variation in the percentage seeding at a site, see text.

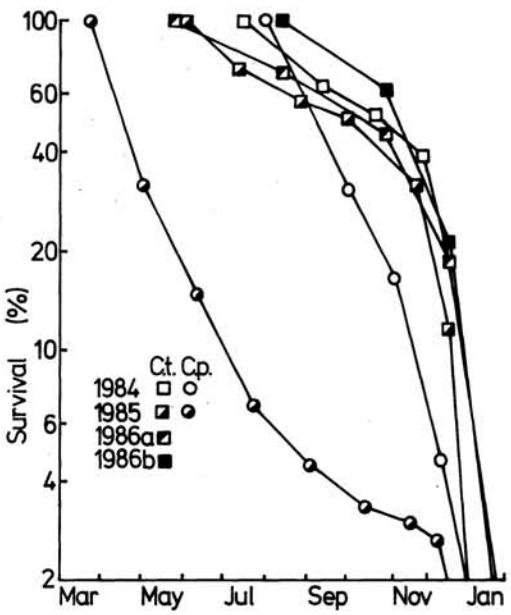

Figure 2. Survival (log scale) of the main autumn cohorts of *Carduus tenuiflorus* at Midland in 1984-86 and *C. pycnocephalus* at Argyll in 1984 and 1985. In 1986 at Midland, germination spanned two censuses, which are both plotted.

indicated higher levels of seed survival than 1.1%. At Midland data for *C. tenuiflorus* were available for three transects over two summers (1984/5 and 1985/6). The estimated germination of seeds in 1984/5 was 7.45%, 11.4% and 15.3% in the three transects; in 1985/6 the estimates were 18.9%, 8.3% and 8.0% respectively. The mean of all six estimates was 11.6%. At Argyll, only two transects were followed in 1985, and only one of these had sufficient numbers of *C. pycnocephalus* to allow seed survival to be estimated. In that transect in 1984/5, seedlings appearing represented 37.8% of the seed crop the year before.

DISCUSSION

LIMITATIONS OF THE DATA

The major difficulty in interpreting these data is the confounding of site, species and weevil attack. The Midland site had only *C. tenuiflorus*, and the Argyll site nearly pure populations of *C. pycnocephalus*; *Rhinocyllus* was only present at Argyll. Therefore it is not possible to conclusively separate the differences which are due to site effects from those due to species differences. The absence of *Rhinocyllus* from Midland is less of a problem, since its effect is only to reduce the number of ripe seeds in an inflorescence, and at Argyll only 16% of inflorescences were attacked by weevils, it is still possible to estimate seed output at the two sites

	C. tenuiflorus			*C. pycnocephalus*	
	1984	1985	1986	1984	1985
Arithmetic mean	22.8	6.52	4.37	9.15	24.6
Back-transformed mean	10.0^{a}	4.11^{b}	2.55^{c}	3.70^{a}	8.99^{b}
Upper 95% C.L. (transf.)	14.0	4.85	3.08	5.73	15.5
Lower 95% C.L. (transf.)	7.14	3.49	2.12	2.39	5.23
N	75	131	89	34	30

Table 2. Mean number of inflorescences per flowering plant for *Carduus tenuiflorus* at Midland and *C. pycnocephalus* at Argyll. Both arithmetic (untransformed) and geometric ($\log_{10}$ transformed) means are presented (see text). Within a species, back-transformed means with the same superscript are not significantly different at the 95% level, according to t-tests.

accurately.

A second limitation of the data is that the estimates of seed survival by difference in the transects assume that there is no net addition to, or germination from, the seed bank. At Midland, where data are available for three transects over two years, additions and subtractions from the seed bank probably average out. However, only a single estimate (from one transect in one year) is available from Argyll, so conclusions drawn from that one datum must be much more tentative.

LIFE CYCLE VARIATION

The germination of both *C. tenuiflorus* and *C. pycnocephalus* was almost completely restricted to autumn. The few seedlings appearing at other times had a lower probability of flowering, and so were of little significance. The same was generally true for *C. nutans* in New Zealand (Popay & Kelly 1986, Popay *et al.* 1987), although *C. nutans* will germinate in large numbers in the spring if pasture cover is removed (Popay & Kelly 1986).

Flower production was very synchronous in the studied populations of *Carduus* spp., with 80% of flowers being produced over the last two weeks of November and the first two weeks of December in every year. Thus, both species behave as typical winter annuals. However, there are records of annual *Carduus* spp. flowering at other times of year. On 18 May 1986 I observed numerous flowering plants in a mixed population of *C. tenuiflorus* and *C. pycnocephalus* on the Bowenvale Walkway, Port Hills, Christchurch. The Botany Division Herbarium has 23 sheets of flowering *C. tenuiflorus* and *C. pycnocephalus* collected in Canterbury; 21 were collected in November or December, one in September and one in May (P. J. Garnock-Jones, pers. comm.). The Auckland Institute and Museum Herbarium has two sheets collected in March and three in October (E. B. Bangerter, pers. comm.).

To understand how these out-of-season flowering plants arose, the control of both flower initiation and germination must be considered. Staig (1986) examined control of flowering in *C. tenuiflorus* rosettes grown indoors in pots from seed collected at the Midland site. Bolting was triggered in all surviving plants both by a change from short days (8 hr) to long days (24 hr) at a constant temperature (21 $\pm$ 3°C), and by a change in temperature (from 21°C initially, to 4°C for 5 weeks, then back to 21°C) at a constant daylength (16 hr).

Therefore it appears that *C. tenuiflorus* will initiate flowering over a wide range of conditions, and the early-flowering herbarium collections (September and October) may represent plants which bolted in response to warm temperatures in early spring. The late flowering plants (March to May) are harder to explain, as normally these thistles are only at the cotyledon

stage at this time of year, if they have germinated at all. I suggest that the late flowering plants must have arisen from seedlings germinating in summer, possibly only in unusually wet summers. Given enough moisture, these seedlings would grow rapidly in the warm temperatures and begin to bolt before the short days of late autumn. March 1986 was wetter than normal in Christchurch, which ties in with the flowering observed on the Port Hills on 18 May 1986. If these plants arose in this manner it would be particularly interesting, because it would mean that the normally-annual plant had in fact completed two generations in a single year (assuming that viable seed is set on autumn-flowering plants). This phenomenon has not to my knowledge been reported elsewhere. The nearest comparable situation is that of ephemerals growing in much less seasonal desert habitats (Tevis 1958).

DIFFERENCES BETWEEN C. *TENUIFLORUS* AND *C. PYCNOCEPHALUS*

There were a number of differences between these two species in their population dynamics, but nearly all these differences could plausibly be attributed to site differences (with the exception of seed weight). *C. pycnocephalus* at Argyll had higher survival from seed to seedling (according to the one available estimate), but lower survival from seedling to flowering, than *C. tenuiflorus* at Midland. The higher rainfall over summer in the Manawatu generally means that the pasture perennials stay green all year, whereas in Hawkes Bay the pasture usually dies right off in the height of summer. The lack of ground cover would be expected to enhance germination in these two species, as has been shown for *C. nutans* (Popay & Kelly 1986). In contrast, the lower soil moisture levels in Hawkes Bay in autumn leads to higher death rates for seedlings and rosettes.

The effect of dense pasture cover on germination may also account for the variable estimates of seed survival at Midland. Where seed was sown into a randomly chosen area (which happened to have a dense grass cover) much lower germination was seen than in the transects nearby, which had more open pasture.

Inflorescence number per plant was variable between years over a similar range for both species. There was no difference between *C. tenuiflorus* and *C. pycnocephalus* in seed number per inflorescence (for a given number of inflorescences per plant) according to the regression analysis. The variation in seed number per inflorescence as a function of inflorescence number per plant parallels the situation in small annuals and biennials, which vary the number of seeds per fruit in a similar way (Kelly 1984).

Overall, the two species are clearly similar in their population biology, although it is not possible to definitely separate site and species effects, or to test the hypothesis statistically, in this particular study.

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